

A reconstruction of the Lava mouse (*Malpaisomys insularis*), an extinct rodent of the Canary Islands

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Abstract

Described the skeleton and evaluated the form, size and ecological niche of *Malpaisomys insularis*, an extinct rodent of the Canary Islands. The lava mouse was a generalized murid rodent with a head and body length of about 110 mm and a slightly shorter tail. Fore and hind limbs exhibit some adaptations for climbing, a favourable condition in its main habitat, the malpaís. There is a notable convergence in skeletal proportions between the lava mouse, the rock mouse (*Apodemus mystacinus*), the Galapagos rice rat (*Nesoryzomys narboroughi*), and other petricolic rodents which share(d) a similar crevicular habitat. The reasons for the extinction of *Malpaisomys* remain obscure. Data from Fuerteventura show that house mice arrived shortly before 2000 B. P.; from that time on to present a population decline of *Malpaisomys* and a contemporaneous increase of *Mus* is documented. Possibly the newly arrived house mice carried a disease which may have contributed to the extinction of the native mouse. This is indirectly suggested by a recently described rodent flea, for which the lava mouse may have been the original host rather than the introduced house mouse.

Introduction

The lava mouse (*Malpaisomys insularis*) is an endemic Canarian rodent recently discovered in subfossil deposits and archaeological sites of Fuerteventura, Lanzarote and Graciosa (HUTTERER et al. 1988). Together with the shrew *Crocidura canariensis*, this rodent formed the native Holocene terrestrial small mammal fauna of the eastern Canary Islands. Two thousand years ago *Malpaisomys insularis* was extremely common, at least in Fuerteventura, where innumerable bones were recovered in the Cueva Villaverde (HUTTERER et al. 1988). It is not known why such a successful rodent became extinct within a few centuries, even more because obvious causes such as competition with the black rat do not hold; our data document the absence of black rats during the extinction process. In order to understand what happened in the past, we have analysed the isolated bones of *Malpaisomys* and, by comparison with a variety of extant rodent species, tried to gain some information on its lifestyle from them. The aim of this paper therefore is first to present a skeletal reconstruction of the lava mouse, secondly to establish its morphological adaptations and to evaluate its ecological niche, and finally to consider the problem of its extinction.

Material and methods

The main part of the skeletal material of *Malpaisomys* used during this study was collected in July 1988 by three of us (R. H., N. L.-M., J. M.) during an excavation of the Cueva Villaverde (Fuerteventura), a project directed by the archaeologists F. HERNÁNDEZ and M. D. SÁNCHEZ. We used dry and wet screening with meshes of three different sizes. In addition we used the material already mentioned in the description of the genus (HUTTERER et al. 1988). After cleaning and sorting representative samples of the larger skeletal bones were measured, as shown in Figure 1. Camera lucida drawings were made from well preserved bones and used for the reconstruction of the skeleton (Fig. 1). As all our material

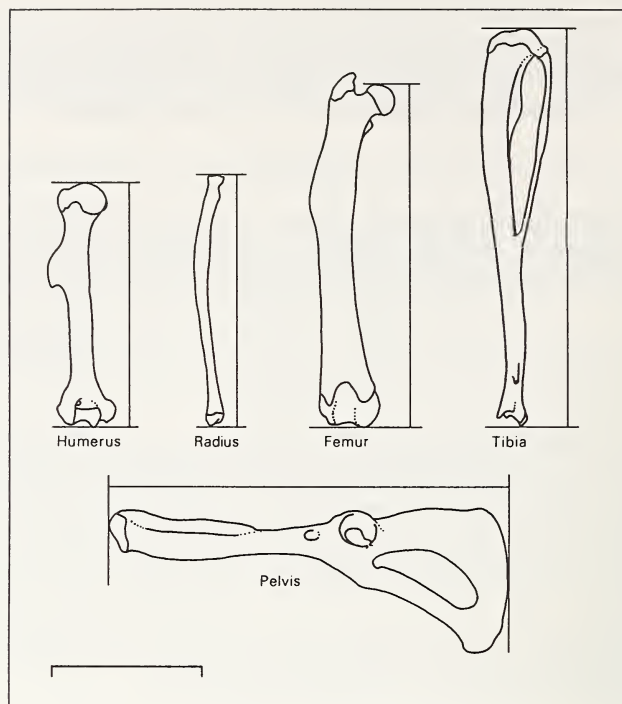


Fig. 1. Definitions of the main measurements taken for this study. Drawn after material of *Malpaisomys insularis* from Fuerteventura. (Scale = 10 mm)

consists of isolated bones, the number of vertebrae could not be accurately determined; however, there is no reason to believe that *Malpaisomys* deviates from other Murinae which normally have 7 cervical, 13–14 thoracic, 6–7 lumbar and 2–4 sacral vertebrae (NIETHAMMER and KRAPP 1978; CARLETON and MUSSEY 1984). For the purpose of comparison skeletons of 14 extant rodent species were prepared and measured (see Table); some data were also taken from RAUSCH (1976) and from BOYE (1988). Complete skeletons of fossil Muridae are very rare; we studied an almost complete skeleton of *Paraethomys* cf. *miocaenicus* from Upper Miocene diatomites of Hellin, Spain (figured in CALVO et al. 1978) in the collections of the Department of Palaeontology, University of Madrid, and we used the information on the Pliocene *Apodemus atavus* given by RIETSCHEL and STORCH (1974). For a description and nomenclature of the bones of the postcranial skeleton of a rodent we refer to SCHICH (1971).

Results and discussion

Size and form of *Malpaisomys*

The lava mouse was large, comparable in body size with the rock mouse *Apodemus mystacinus*. Our reconstruction of the skeleton (Fig. 2) shows an animal of about 110 mm head and body length. The vertebral column is little modified and the dorsal and lateral processes are small. The processus spinosus of the epistropheus is rather small. A hypertrophied neural spine is not present on the second thoracic vertebra. There are three sacral vertebrae, the first two of which are usually fused. Their transversal appendices leave space for two pairs of round foramina sacralia.

Scapula, humerus, radius and ulna are similar to any species of *Apodemus*, except for their dimensions which will be discussed below. The same applies to the pelvis, femur and tibia. The tibia appears rather long and the crista tibialis is strongly developed, apparently

providing space for a large *musculus flexor hallucis* and *musculus flexor digitorum*, both of which are responsible for the flexibility of the toes. Also the *musculus popliteus* inserts at the *crista tibialis*. This muscle counteracts a rotation in the knee-joint, which is advantageous for a climbing animal. 54.3 % of the fibula length are not fused with the tibia.

The hindfoot length is difficult to estimate from isolated bones, but judged from the length of the calcaneus and the metatarsale (Fig. 2), it may have been about 26 mm.

Estimation of the tail length presented a problem. We finally found a simple solution for this problem, as demonstrated in Figure 3: plotting the known tail length of 14 species of murids (see Table) against the width of the second sacral vertebra (where tail-supporting muscles insert) gives a clear linear relation, which afterwards could be used to estimate the unknown tail length of *Malpaisomys* and other extinct rodents. For the lava mouse (mean width of the second sacral vertebra = 6.1 mm) we estimated a tail length of ca. 105 mm.

The body weight of the lava mouse was about 40 g. This calculation is based on the relation between head and body length and body weight of 34 species of European rodents (raw data were taken from NIETHAMMER and KRAPP 1978, 1982). The relation is highly significant ($r^2 = 0.95$, $n = 34$); a calculation for a head and body length of 110 mm resulted in a body weight of 37.9 g, which is very near to the weight of *Apodemus mystacinus* (40.9 g).

Biological data

In a previous paper (HUTTERER et al. 1988) we have mentioned that length measurements of 100 mandibles of lava mice show a bimodal distribution, if age classes are treated separately, which indicates a pronounced sexual dimorphism. There is more evidence for this assumption in the skeleton: the pelvis shows the same differences in shape (Fig. 4) that BECKER (1954) described for males and females of 8 European mice and voles. The os pubis is prolonged in females, while in males it is shorter and the ischium is broader.

Of the mandibles (from a level older than 1730 B.P.) measured, 27.8 % were classified as belonging to age class 1 (juvenile), 55.5 % to age class 2 (subadult to adult) and 16.7 % to age class 3 (old adult). We found similar values for *Mus musculus* from recent owl pellets from Lanzarote: of 100 mandibles 33 % belong to age class 1, 58 % to age class 2 and 9 % to age class 3. As the present-day house mice in the Canary Islands live in evidently viable

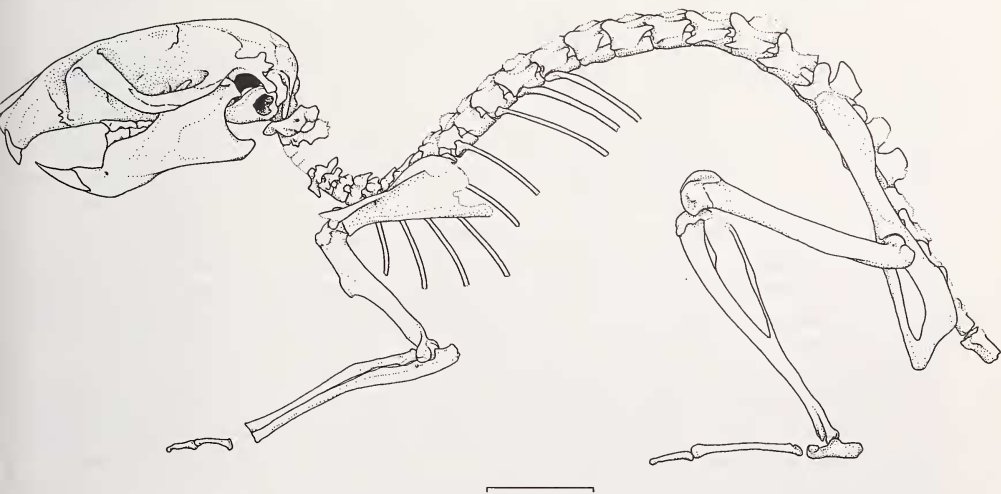


Fig. 2. Skeleton of the lava mouse *Malpaisomys insularis*, reconstructed from isolated bones from Cueva Villaverde, Fuerteventura. All elements shown have been found; most of the tail has been omitted. (Scale = 10 mm. Drawn by P. BOYE)

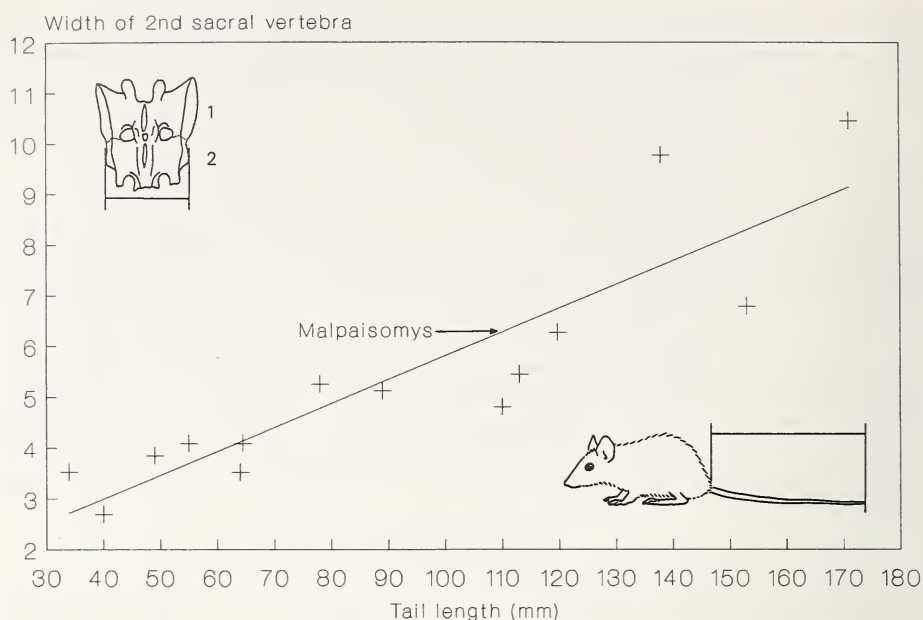


Fig. 3. The relation between tail length and width of the second sacral vertebra in 14 species of extant rodents; the width of the second sacral vertebra in *Malpaisomys* points to a tail length of about 105 mm

populations, we may draw the same conclusion for the ancient population of the lava mouse. At least we found no evidence for a limited viability, also no teratological bones and no tooth malformations. However, we have not yet sorted and examined all the material from all levels of the cave; therefore these comments must be taken as preliminary.

Foraging category and ecological niche

The skeleton of the lava mouse seems to represent a rather general type of murid with no special adaptations. However, if we compare its limb proportions with a set of living rodents for which the ecology is known, the picture becomes different. Figure 5 shows the relation between head and body length and the physiological fore limb length (humerus + radius) and hind limb length (femur + tibia) for a population of the terrestrial *Mus musculus*, and for two species of petricolic rodents, the Spiny mouse *Acomys dimidiatus* and the rock mouse *Apodemus mystacinus*. The diagram shows that both fore and hind limbs are relatively longer in the petricolic mice, and longest in the rock mouse, a species which lives in karstic rock fissures of the Mediterranean and Asia Minor. The petricolic snow vole *Microtus nivalis* (not shown in figure) also groups nicely near *Acomys* and *Apodemus mystacinus*; this vole is a good climber in rock fissures (BOYE 1989).

The mean values for *Malpaisomys* fall into the range of *Apodemus mystacinus*. The same applies to *Nesoryzomys narboroughi* (not shown in the graph), a lava-dwelling rat endemic to the Galapagos Islands. We have compared the limb bones of *Malpaisomys* with those of *Nesoryzomys* and *Apodemus mystacinus* and found them to be very similar. The bones of *Nesoryzomys* (a member of the Sigmodontinae) are somewhat more heavily built, but those of *A. mystacinus* and *Malpaisomys* are almost indistinguishable.

Subterranean or fossorial rodents (Table; not shown in the graph) group far below the line for the terrestrial *Mus musculus*.

Selected measurements of skeletal elements

Species	Pelvis	Femur	Tibia	Humerus	Radius	HB	n
unclassified extinct species							
<i>Malpaisomys insularis</i>	26.2	22.4	25.5	16.4	17	(110)	4–20
<i>Paraethomys miocaenicus</i>	17.2	16.7	20.6	12.0 scansorial	13.1	(105)	1
<i>Micromys minutus</i>	11.8	10.0	13.3	8.2	8.9	62.9	2
<i>Grammomys caniceps</i>	19.1	17.3	20.8	13.1	12.5	97	2
<i>Apodemus sylvaticus</i>	16.9	16.1	20.6	12.4	12.3	90.1	8
<i>Apodemus flavicollis</i>	22.1	20.3	25.0	15.5 petricolic	15.3	107.5	2
<i>Apodemus mystacinus</i>	23.6	22.5	27.8	16.6	16.9	111.7 ^a	15
<i>Acomys dimidiatus</i>	21.7	18.8	22.3	14.3	13.4	105	1
	–	19.4	22.0	15.1	14.1	104.6	20 ^b
<i>Microtus nivalis</i>	21.2	17.9	21.9	15.4 terrestrial	14.7	113.9	11
<i>Mus musculus</i>	15.5	12.8	15.8	10.0	10.4	73.5	1
	–	15.5	18.1	12.3	11.4	93.3	20 ^b
<i>Microtus agrestis</i>	16.8	13.7	17.8	12.4	12.0	98.7	14
<i>Clethrionomys glareolus</i>	16.5	13.9	17.8	12.4	11.5	91.3	7
<i>Apodemus agrarius</i>	13.5	14.7	17.8	11.6	11.2	93	2
<i>Arvicanthis niloticus</i>	38.5	30.9	32.4	22.9 fossorial	20.7	174.3	4
<i>Spalax leucodon</i>	27.5	21.5	22.1	21.2	17.2	170	1
<i>Arvicola terrestris</i>	27.2	21.2	23.7	18.8	16.7	138	1

^a NIETHAMMER and KRAPP (1978). – ^b Laboratory strains (RAUSCH 1976).

The Miocene rodent *Paraethomys* cf. *miocaenicus* (Fig. 5) goes along with *Mus*, as does the Pliocene *Apodemus atavus* (not shown in figure) for which species we took the measurements from RIETSCHER and STORCH (1974). These two extinct species show a rather unspecialized condition, which we regard as primitive within the Muridae. This does not necessarily mean that all fossil rodents were primitive; SCHMIDT-KITTLER and STORCH (1985) described a skeleton of an Oligocene ‘sand rat’, *Pseudoltinomys* (Theromomyidae), and KOENIGSWALD et al. (1988) showed that in the Eocene there lived already highly specialized arboreal rats such as *Ailuravus* (Paramyidae).

The limb proportions of *Malpaisomys* strongly suggest that the species was a good climber in rock fissures. This coincides perfectly with the sites where we found fossils of lava mice in the Canary Islands. Most were in somewhat weathered lava fields of Tertiary or Quaternary age, for which the Canarian people use the term ‘malpaís’. Our main locality, the Cueva Villaverde, is a lava tube in the midst of such an ancient lava field. Only

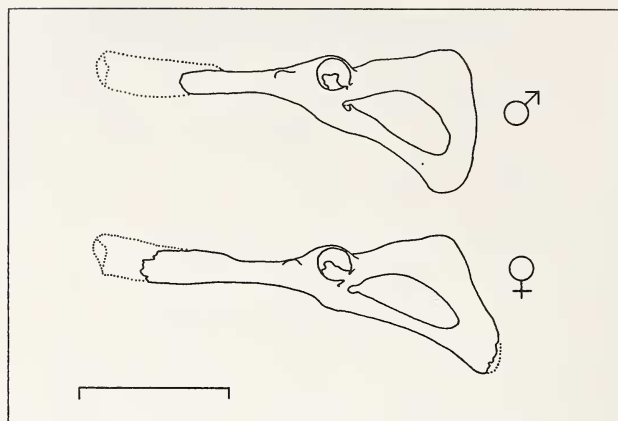


Fig. 4. *Malpaisomys insularis*, sexual dimorphism in the shape of the pelvis. Material from Malpais de Arena, Fuerteventura. (Scale = 10 mm)

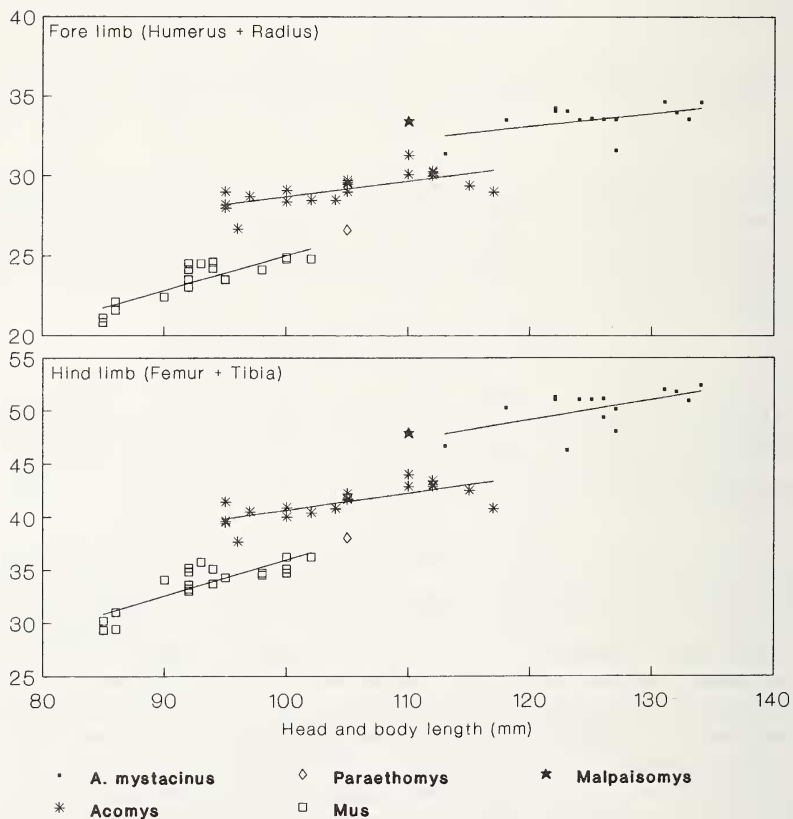


Fig. 5. Head and body length plotted against fore and hind limb length for populations of *Mus musculus*, *Acomys dimidiatus* (data from RAUSCH 1976) and *Apodemus mystacinus* (own data); the values for *Malpaisomys insularis* and the Miocene *Paraethomys* cf. *miocaenicus* are indicated

two localities in the Jandia peninsula (Fuerteventura) are different; there the fossils were found below a steep cliff, in the upper parts of which relict plants grow which are dependent upon high humidity. At the base of this mountain cliff there are large rock rubble piles which would provide a suitable fissure system for petricolic small mammals. However, traps set there for small mammals in July 1989 by one of us (R. H.) yielded no catches at all. In another locality in the Jandia peninsula we found fossils of lava mice in Pleistocene dunes (MICHAX et al. 1991).

There is no indication that the former habitat of *Malpaisomys* was much different from the present-day malpais. We therefore hypothesize that the species had its ecological niche in the malpais zones of Fuerteventura, Lanzarote and adjacent islets, and that its morphological adaptations favoured living and climbing in the creviscular system of the lava fields. It only had to share this habitat with the endemic shrew *Crociodura canariensis* (HUTTERER et al. 1987), at least until the date when the house mouse arrived.

The extinction of *Malpaisomys*

From our most ancient fossil localities in Fuerteventura and Lanzarote we know that the native terrestrial small mammals of the eastern Canary Islands were *Malpaisomys insularis* and *Crociodura canariensis* (HUTTERER et al. 1988; MICHAX et al. 1991). Our oldest samples from the Cueva Villaverde comes from a level underlying a horizon dated 1730 B.P. (HERNÁNDEZ and SÁNCHEZ 1986; CARRASCOSA and LÓPEZ-MARTÍNEZ 1988); in this sample *Malpaisomys* constitutes 58.9% of the mammals, *Crociodura canariensis* 38.9%, and *Mus musculus* 2.2%. In the levels of younger age the proportion of *Mus* increases drastically (CARRASCOSA and LÓPEZ-MARTÍNEZ 1988), although no quantitative counts of all mammals are available for the moment. However, the data are sufficient to show that House mice occurred in Fuerteventura in very low numbers at 1730 B.P., and that they presumably arrived in the island a few centuries before, say 2000 B.P.

This was approximately the time when man arrived in the Canaries from neighbouring Africa. ONRUBIA PINTADO (1987) has shown that there are no absolute datings of archaeological sites in the Canaries older than 2490 B.P. (Tenerife: Barranco Hondo) and 1890 B.P. (Gran Canaria: Los Caserones). A fossil dune deposit with remains of endemic Giant rats, but without archaeological context (erroneously cited as such by ONRUBIA PINTADO 1987) at La Aldea, Gran Canaria, was dated as 2080 ± 60 B.P. (Cologne Radiocarbon Laboratory reference number KN-3542; this date was mentioned without source by LÓPEZ-MARTÍNEZ and LÓPEZ-JURADO 1987). This dune deposit also yielded one skull and one mandible of *Mus musculus*, which further supports our assumption of the arrival of house mice in the Canary Islands around 2000 B.P. The contemporary arrival of man strongly suggests a casual import of mice with ships from Africa.

Figure 6 shows that in a sample from historical times (ca. 800 B.P.; goat and rabbit were already present) the percentage of *Malpaisomys* is only 10.9% while that of *Mus* is now 60.7%. In two modern barn owl pellet collections shown in the same figure, the percentage of *Mus* is 95 and 87.4%, while *Malpaisomys* is absent.

From our yet limited data we conclude that the populations of the lava mouse declined since the arrival of house mice about 2000 years ago, and were progressively replaced by them. We also show that black or brown rats (*Rattus rattus*, *R. norvegicus*) were not present during the extinction process, and – surprisingly – are even absent in recent owl pellets from arid regions of Fuerteventura. Today the black rat exists in Fuerteventura in cultures and villages, but seems to avoid the open plain and the lava fields. Apparently it was introduced quite recently.

Our present data suggest that for almost two millennia *Malpaisomys* and *Mus* were the only rodents in Fuerteventura. It is therefore possible that interactions between these two species have caused the extinction of the lava mouse. Other factors like climatic changes or

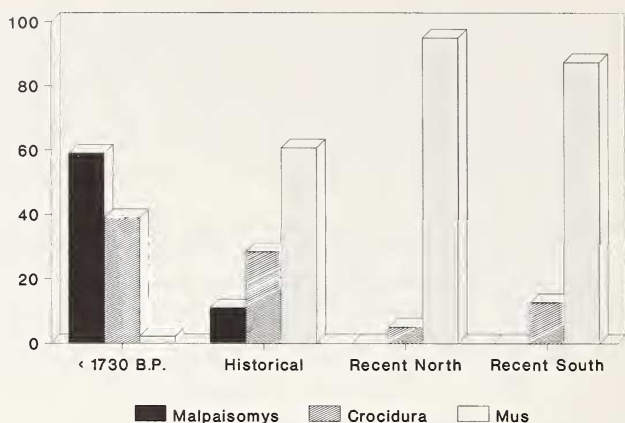


Fig. 6. The percentages of micromammals in fossil and recent barn owl pellets from Fuerteventura. From left to right: Cueva Villaverde, level older than 1730 B.P. ($n = 764$); Malpais de Arena, Historical period, ca. 800 B.P. ($n = 183$); Villaverde, recent barn owl pellets ($n = 240$); Barranco de la Torre, recent barn owl pellets ($n = 111$)

volcanic activities may have added to this process, but these variables are unsufficiently documented. However, CARRASCOSA and LÓPEZ-MARTÍNEZ (1988) have shown that the house mouse suffered some loss in size from about 2000 B.P. to present, which indicates environmental changes. On the other hand the shrew *Crocidura canariensis* survived from the Pleistocene (MICHAX et al. 1991) into our times and still occurs in high numbers in the malpais.

What remains is the fact that the numbers of lava mice declined and those of house mice increased. Direct competition between the two rodents seems unlikely, as they represent two distinct size classes. We consider the possibility of an indirect impact of house mice on lava mice, for example through a fatal disease carried by the house mice and consequently transmitted to the formerly isolated lava mice.

Indirect evidence for a contact between both may be taken from a paper on fleas of extant Canarian rodents by BEAUCOURNU et al. (1989). They described a new flea, *Xenopsylla guancha*, which they collected from house mice in Lanzarote; it was not found in other islands of the archipelago and not previously in the (well-studied) north-western parts of Africa. According to the authors, the new flea is related to North African species for which gerbils are the main hosts; therefore they discuss the possible existence of a vanished gerbil in the Canaries.

According to our data house mice arrived in the Canary Islands only 2000 years ago. There is no evidence for gerbils but for *Malpaisomys* in Lanzarote and Fuerteventura. Probably the lava mouse was the original host of the flea *Xenopsylla guancha*, which later changed to the house mouse and survived there after its native host had vanished.

Acknowledgements

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Zusammenfassung

Eine Rekonstruktion der *Lavamaus* (*Malpaisomys insularis*), einem ausgestorbenen Nager der Kanarischen Inseln

Anhand von subfossilen Knochenresten wurde das Skelett der *Lavamaus Malpaisomys insularis* rekonstruiert und ihr Körperbau, ihre Körpergröße und ökologische Nische abgeschätzt. Die *Lavamaus* entsprach einem generalisierten Muriden; die Kopf-Rumpflänge betrug ca. 110 mm, der Schwanz war etwas kürzer. Die Vorder- und Hinterextremitäten waren verlängert, eine Anpassung an die kletternde Lebensweise in den Lavawüsten der Kanarischen Inseln. Die Skelettproportionen sind bemerkenswert ähnlich denen der Felsenmaus (*Apodemus mystacinus*), der Galapagosreisratte (*Nesoryzomys narboroughi*) und anderer felsbewohnender Nager, die ebenfalls in dreidimensionalen Habitaten leben. Die Gründe für das Aussterben der *Lavamaus* in historischer Zeit sind unklar. Daten aus Fuerteventura belegen, daß die Hausmaus (*Mus musculus*) auf dieser Insel um 2000 B.P. eintraf; von da an läßt sich in subfossilen Eulengewöllen eine Abnahme von *Malpaisomys* und eine Zunahme von *Mus* belegen. Möglicherweise infizierten Hausmäuse die Lavamäuse mit unbekannten Krankheiten; indirekt weist darauf ein nur von Lanzarote bekannter Floh hin, der von Hausmäusen abgesammelt wurde. Da Hausmäuse erst in historischer Zeit dort eingewandert sind, kommt als natürlicher Wirt nur die *Lavamaus* in Frage.

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